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NEW OR LITTLE-KNOWN UNGULATES FROM THE *PYRO- THERIUM* AND *COLPODON* BEDS OF PATAGONIA¹

BY GEORGE GAYLORD SIMPSON

In a previous paper of this series² some preliminary notes on fossil mammals from the *Colpodon* Beds were published. As there explained, revision of the *Pyrotherium* and *Colpodon* faunas is being undertaken at the Field Museum, and that of the *Notostylops* and *Astraponotus* faunas at the American Museum, but each is publishing some preliminary notes on some of its material which will be definitively treated at the other institution. The paper cited accordingly discussed some marsupials, edentates, and rodents from the *Colpodon* Beds, and the present paper similarly deals with some new ungulate specimens. The next communication will be devoted to the typothere genus *Cochilius*, and will be the last of this series to describe specimens later than the *Astraponotus* Beds. The drawings in this paper are by Mildred Clemans, and again I am indebted to Professor W. B. Scott for permission to publish photographs taken by him.

LITOPTERNA

Proterotheriidae

Deuterotherium distichum Ameghino, 1895

Amer. Mus. No. 29554, found by me in the *Pyrotherium* Beds of Cabeza Blanca, is referred to this species. It consists of several skull fragments, incomplete but permitting a reasonably probable restoration, and thus adding significantly to our knowledge of pre-Santa Cruz litopterns.

The anterior part of the palate is poorly preserved. There are notches that may be alveoli, but they are too uncertain to be of any value. If alveoli, they indicate smaller and more numerous incisors than in later proterotheres. Ameghino stated that the dental formula was as in Santa Cruz proterotheriids, i.e. (by the standard notation, not Ameghino's), $\frac{1.0.4.3}{2.1.4.8}$, but this was based on a lower jaw, and he does not appear to have had anterior upper teeth. In any event, *Deuterotherium* did have at least one upper tooth not allowed for in this formula, either

¹Publications of the Searritt Patagonian Expedition, No. 8.

²Amer. Mus. Novitates, No. 575.

I³ or C, a small, one-rooted tooth present on the left side of our specimen.¹ From this, a less certain general impression of the poorly preserved anterior end, and Ameghino's statements regarding the lower jaw, it appears that the diastemata were much shorter in *Deuterotherium* than in the Santa Cruz genera (except possibly *Thoatherium*) and that the incisors generally were less specialized. P¹ is lacking in the specimen, P² is badly worn, but has the long narrow triangular outline and more posterior internal heel of P¹ in the Santa Cruz, except in *Thoatherium*. P³ was similar to P⁴ but slightly less transverse and with smaller hypocone. The succeeding teeth have been described and figured by Ameghino, from a less worn specimen. The distinctive characters are

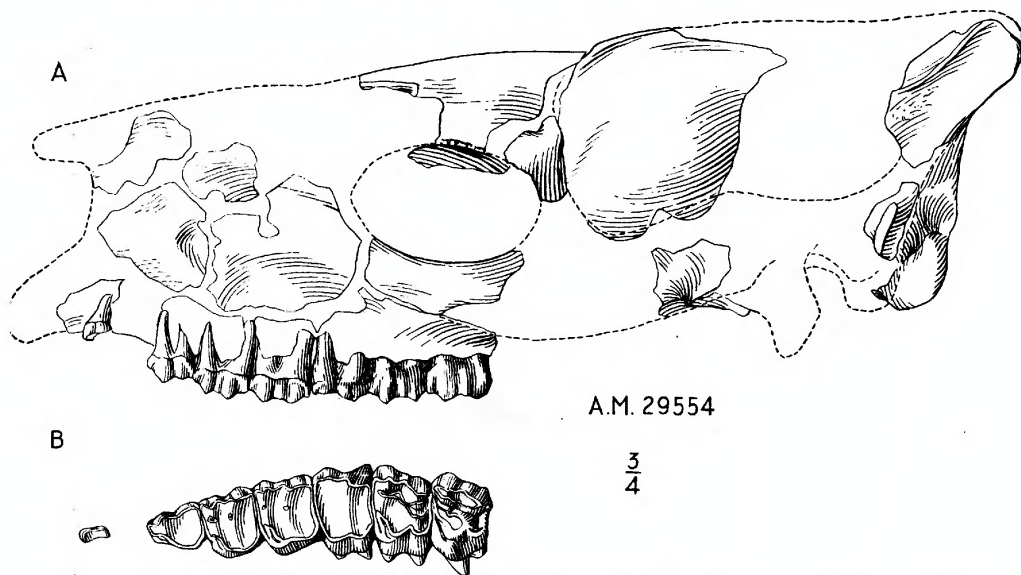


Fig. 1—*Deuterotherium distichum* Ameghino. Skull, Amer. Mus. No. 29554. A, Reconstruction of left lateral view, some parts reversed from other side. B, Left teeth, crown view. Three-fourths actual size.

the partly confluent but oblique protoconule—protocone—hypocone, relatively strong hypocone of M³, absence of metaconule, weak external crests and no external cingulum, well developed anterointernal but no truly internal cingulum. Ameghino stated that the internal roots are separate here and fused in the Santa Cruz. They are more nearly equal in *Deuterotherium*, but they are not completely fused in such Santa Cruz specimens as I have examined.

¹Id³ is sometimes present in young *Thoatherium*. The present individual is, however, old.

The frontal and parietal regions resemble those of Santa Cruz proterotheres, which differ among themselves only in rather minor and variable details. From the preserved postorbital process of the frontal, it appears that the orbit was already closed, and the characteristic foramina in the frontal are already present. In exact relationship, this region seems a little closer to *Proterotherium* than to *Thoatherium*, but the known differences are too slight to be significant. Much more important and definite is the occiput, which in *Deuterotherium* is of the characteristic *Thoatherium* type, high, steeply inclined, pointed above, with strong lambdoid crest flaring backward, not outward.

Ameghino, Loomis, Scott and, following them, all other authorities have placed *Deuterotherium* in the Proterotheriidae. It is clear that the early proterotheres as they may be discovered, and probably including this genus, will not possess in the same degree the characteristic rostral protrusion, long diastemata, and rodent-like incisors which are commonly cited as defining the Proterotheriidae. The easy separation of the litoperns into those with diastemata (proterotheres) and those without (macraucheniids) in the Santa Cruz will not hold in the earlier formations. There are, as was to be expected *a priori*, genera in the *Notostylops*, *Astraponotus*, and *Pyrotherium* Beds (e.g., *Xesmodon*, *Protheosodon*) that would be, and in some cases have been, placed in the Macraucheniiidae on this basis but which from the molar structure and other features probably do not really belong there.

Regardless of how far it may have progressed in the specialization of the anterior dentition, molar and skull structure seem fully to warrant retaining *Deuterotherium* in the Proterotheriidae. Its closer relations within that group can be established with some probability.

The essential upper cheek tooth characters of the four definitely established Santa Cruz genera (Scott and original specimens) are:

Diadiaphorus.— P^{2-4} with hypocone strongly developed. On molars, protocone and protoconule partly confluent and ridge strongly oblique. Hypocone nearly separate. Metaconule present. Hypocone very small on M^3 . Weak external, strong internal cingula.

Licaphrium.—Hypocone incipient on P^3 , absent on P^2 and P^4 . On molars, protocone and protoconule nearly as in *Diadiaphorus*. Hypocone less separate. Metaconule present. Hypocone present on M^3 . Cingula variable, weaker internally than in *Diadiaphorus*.

Proterotherium.—Hypocone indicated on P^3 , present on P^{3-4} but less separate than in *Diadiaphorus*. On molars, protocone, protoconule, and hypocone about as in *Diadiaphorus*. Metaconule present. No hypocone on M^3 . Strong external, weak internal cingula.

Thoatherium.— P^2 without hypocone and smaller internal heel than in other genera; P^{3-4} with nearly connate hypocones. On molars, protocone, protoconule, and hypocone forming nearly continuous anteroposterior crest. Metaconule absent or indistinct. Hypocone present on M^3 . No external or truly internal cingula.

Of these, *Deuterotherium* is more easily interpreted as a forerunner of *Thoatherium* than of any of the other genera. It agrees in the following points:

1. Shape and development of P^2 —more like P^1 of the other genera.
2. Presence of hypocone on P^{3-4} .
3. Molar protoconule-protocone-hypocone more oblique and separate than in *Thoatherium*, comparable to *Licaphrium*, but a probable condition in the ancestry of *Thoatherium*.
4. Absence of metaconule.
5. Relatively strong hypocone on M^3 .
6. No external or strictly internal cingula.

To these points of agreement are to be added the suggestion that in both *Deuterotherium* and *Thoatherium* the antemolar teeth are less reduced, the fact that they are less specialized and the still more positive agreement in the distinctive structure of the occiput. Against them there is little to cite except Ameghino's statement (1897, p. 48 of the separate) that "les molaires inférieures portent une tubercule interne dans le creux postérieur interne comme dans le genre *Licaphrium*, mais la dernière molaire inférieure n'a pas de troisième lobe." But in *Licaphrium* it is only in the development of a "third lobe" on M_3 that the molars differ really markedly from those of *Thoatherium*, so that this does not very strongly oppose relationship to the latter.

On this aggregate of evidence, it seems probable that *Deuterotherium* is most closely related to *Thoatherium* among the Santa Cruz genera, and possible that the relation is rather directly ancestral.¹

TYPOTHERIA

Interatheriidae

Cochilius fumensis,² new species

TYPE.—Amer. Mus. No. 29551, partial skull and lower jaws with dentition nearly complete. Found by Justino Hernández.

HORIZON AND LOCALITY.—*Pyrotherium* Beds?, west side of the meseta of Cerro del Humo, north of Lago Musters, Chubut, Argentina.

DIAGNOSIS.—Length P^1 – M^3 , 34 mm. P^{1-2} but little longer than wide. P^1 not distinctly grooved, P^2 ridged and grooved externally, much like P^{3-4} , but without distinct internal sulcus.

¹Loomis (1914, pp. 30–31) reached the same general conclusion on a review of Ameghino, without additional original material, but he states that the separation of protocone and protoconule occurs also in *Thoatherium* (his "*Thoatherium*"), whereas they are really united in that genus—not a resemblance but one of the few points of contrast.

²*Fumus*, smoke, for the locality, Cerro del Humo.

The type was found in a bed of very hard silicified pink tuff, and the only associated fossils were two partial lower jaws of the same species, some molds of *Strophocheilus* sp., and some dubious impressions or concretions. The direct palæontological evidence of its age is thus very incomplete. *Strophocheilus* occurs at all pre-Patagoniano Tertiary horizons. *Cochilius fumensis* is close to *C. volvens* of the *Colpodon* Beds, but on the other hand it is also clearly related to *Archæophylus patrius* of the *Pyrotherium* beds, and it is very possible that *Archæophylus* and *Cochilius* are synonymous. Its age should be either *Pyrotherium* or *Colpodon*. The stratigraphic evidence is also imperfect. The outcrop

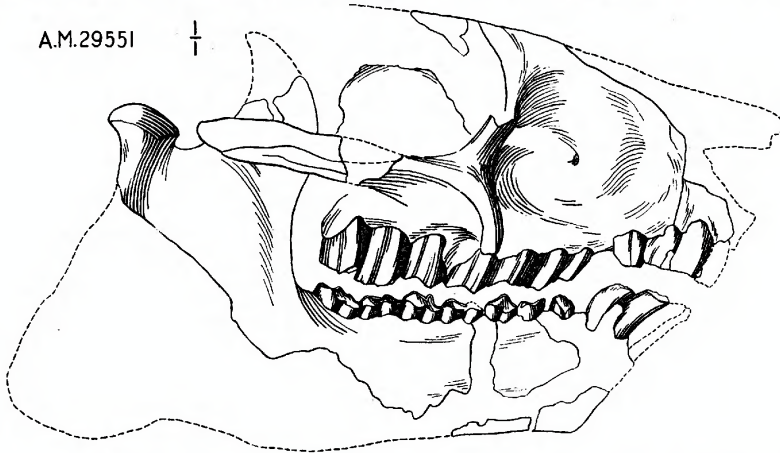


Fig. 2—*Cochilius fumensis*, new species. Type, Amer. Mus. No. 29551. Right lateral view of skull and lower jaw. The posterior part of the mandible, median fragment of zygomatic arch, and P_1 are reversed from the other side. Natural size.

Fig. 3—*Cochilius fumensis*, new species. Type, Amer. Mus. No. 29551. Crown view of right upper teeth. Natural size.



is an obscure one in folded and faulted strata. Nearby but in a bed of different character was found a jaw of *Pyrotherium romeroi* and isolated teeth of *Parastrapotherium* sp., definitely indicating *Pyrotherium* age. It appears probable that the present type was at a horizon somewhat higher than these, but in or closely associated with the same series, so that it probably is from the *Pyrotherium* Beds, although the possibility of later age is not wholly excluded.

Ameghino named three genera in the *Pyrotherium* fauna with cheek teeth comparable to those of this specimen, with unreduced dentition,

and incisors rooted and not much enlarged: *Archæophylus*, *Argyrohyrax*, and *Plagiarthrus*. The first he referred to the Protypotheriidae (= Interatheriidae), the latter two to the Archæohyracidae. Loomis separated the genera still farther, removing *Argyrohyrax* to the Eutrachytheridae. He considered *Plagiarthrus* as possibly representing the lower dentition of that genus, although he placed them in different families.

In this last surmise I think Loomis was almost surely correct. The little that is known of the lower teeth of *Argyrohyrax* is like *Plagiarthrus*. The type species, *A. proavus* and *P. clivus*, appear to be of almost exactly the same size and perfectly harmonious in character. They are probably synonymous, and *Plagiarthrus*, the older name, may be retained in lieu of *Argyrohyrax*. This genus seems to be closer to the Interatheriidae than to the Archæohyracidae or Eutrachytheridae, although the distinctions between these families are by no means so clear-cut as one might wish or as Ameghino and Loomis suggested. Ameghino's figure does not give a wholly adequate impression of the lower teeth of *Plagiarthrus*, and in fact they are hardly distinguishable from those of *Cochilius*, an undoubted interatheriid. Loomis placed the upper teeth, "*Argyrohyrax*," in the Eutrachytheridae because of the bifid internal fold, but in *Cochilius* the fold is bifid in young individuals in just the same way and to about the same degree. These upper teeth differ much more from *Eutrachytherus* than they do from *Cochilius*. The only marked distinctions from the latter are the apparently lower crowns of I¹-C, their stronger internal cingula, and the possible presence of internal enamel. None of these observations is of clear significance and they may even be in part erroneous. In short, it appears that *Plagiarthrus* should be retained tentatively as a genus, but placed in the Interatheriidae.

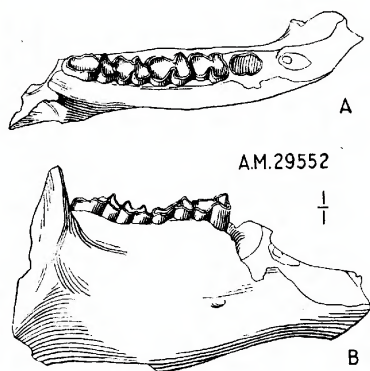


Fig. 4—*Cochilius fumensis*, new species. Topotype, Amer. Mus. No. 29552. Right lower jaw with P₄-M₃. A, Crown view. B, Side view. Natural size.

Archæophylus, based on a palate and unfigured lower jaw, is likewise of dubious status. It is clearly an interatheriid and both Ameghino and Loomis so placed it. The genotype is considerably smaller than any other *Pyrotherium* and *Colpodon* Beds species referred to this family. The only possibly generic distinction from *Cochilius* given by the avail-

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able data is the supposedly rooted premolars. In view of the difficulty of distinguishing milk teeth in this family and of the fact that at least P_1^1 and perhaps also P_2^2 appear to be rooted in *Cochilius*, this supposed distinction is of uncertain value. The genera may be retained as separate tentatively, pending better knowledge of *Archæophylus*.



Fig. 5—*Argyrohyrax proavus* Ameghino. Type. Left upper teeth. Crown view. Natural size. Photograph by Professor W. B. Scott. (The number refers to the negative and is not a catalogue number.)

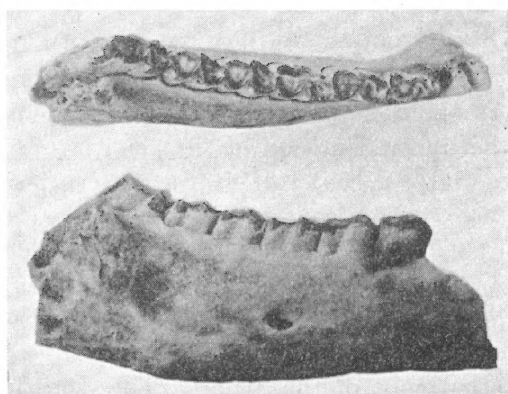


Fig. 6—*Plagiarthrus clivus* Ameghino. Type. Right lower jaw. Crown and side views. About natural size. Photograph by Professor W. B. Scott.

The present species differs from *Plagiarthrus* ("Argyrohyrax"), if that be a valid genus, in the higher I^1-C , without lingual enamel (at least where worn), and from *Archæophylus*, if that be valid, in the rootless P_{3-4} . These are resemblances to *Cochilius*. It differs from most or

some specimens of *Cochilius* in characters surely or probably due to age, such as the non-bifid internal sulcus of the upper molars, failure of anteroexternal groove of upper premolars to penetrate the crown, and absence of posterointernal sulcus on the lower molars. In the first it resembles *Archæophylus*, in the last two *Plagiarthrus*, but I do not believe that these characters have taxonomic value in this case—all may be seen in aged specimens of *Cochilius*. It likewise differs from *Cochilius volvens* in the shorter, wider P_2^2 , but this I take to be a specific character.

In general, the dentition, the facial part of the skull, orbit, and zygoma are remarkably close to *Cochilius volvens*, and whatever the final status of *Archæophylus* and *Plagiarthrus*, the species may best be placed in *Cochilius*.

MEASUREMENTS:—

P^1-M^3 —34 mm.

M^1-M^3 —15.5 mm.

P_1-M_3 —34 mm.

M_1-M_3 —16.5 mm.

TOXODONTA

Rhynchippidæ

***Rhynchippus pumilus* Ameghino, 1897**

Ameghino (1897, p. 464) described and figured a fine skull of this interesting species, and Loomis (1914, p. 95) described and figured skull, jaws, and much of the skeleton of *Rhynchippus equinus*. All previous descriptions of the upper dentition of the genus, however, have been based on deeply worn teeth, so that their true pattern has been unknown.

Amer. Mus. No. 29555, collected by me in the *Pyrotherium* Beds of Cabeza Blanca, Chubut, is a skull referable to this species. The greater part of the skull itself is present, and some interesting features, especially in the auditory region, are visible, but it is badly broken and crushed and these details can be treated more lucidly by broader comparisons beyond the scope of this paper. The dentition is very well shown, is of unusual interest, and will be described here.

The teeth are in almost ideal stages of wear to reveal all their characters. I^1 is well worn but still pitted, I^2 moderately worn, with pattern still clear, and I^3 unworn. The canines are missing. P^1 is formed, but dm^1 is still in place below it. P^{2-3} are slightly worn, with apical pattern still clearly visible, and P^4 has cut the gum but is unworn. M^{1-2} are functioning, with apical cusps all worn off but none of the pits obliterated, the pulp cavities nearly closed and permanent roots forming

M³ is just about to cut the gum, quite unworn, the pulp cavity widely open and the crown not yet fully formed.

Loomis distinguishes this family as brachyodont, but I think the term inapplicable. The molar crowns are more than twice as deep as their greatest anteroposterior diameter and do not form closed roots until after their eruption. They are distinctly hypsodont, although not of continuous growth.

I¹ and I² are both very hypsodont and strongly curved, subequal in size. I³ is somewhat smaller and with a lower crown. Each has a well

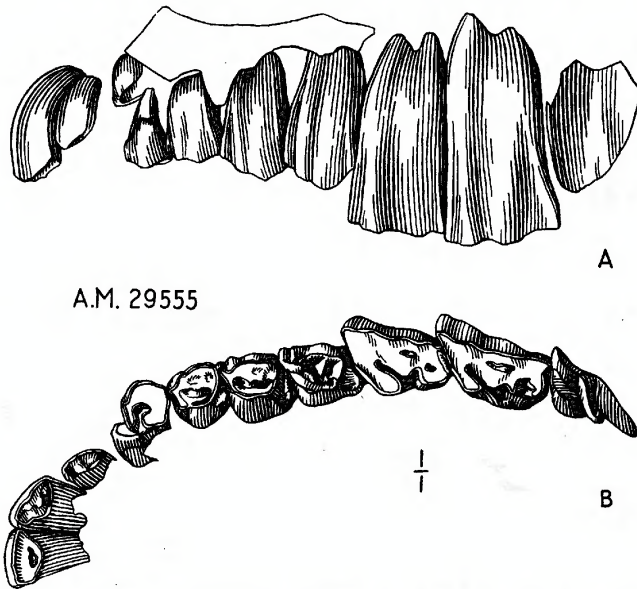


Fig. 7—*Rhynchippus pumilus* Ameghino. Amer. Mus. No. 29555. Left upper teeth. A, Side view. B, Crown view. Natural size.

marked but rather shallow apical pit which on I² and still more distinctly on I³ tends to open through a narrow notch at the lateral or posterior (proximal) edge. At least on I²⁻³ there is a small rounded ridge within the pit, fully united with the middle of the external crest. On I² it is short, simple, and ends freely in the pit. On I³ it is a more formless low rounded eminence filling most of the bottom of the pit. P¹, not fully visible on our specimen, seems to resemble I³. dm¹ has a much lower and nearly circular crown with a central pit.

P²⁻⁴ are of closely similar structure, progressively increasing in size and in relative height of crown. At first, length exceeds width, but with

increasing wear these dimensions would become nearly equal. The ectoloph is marked by a sharp anteroexternal vertical groove, separating parastyle and paracone ridges, as well as a less marked posteroexternal ridge. The apex, when unworn, is marked by three pits or fossettes, separated by crests. The longest and deepest occupies the inner side and extends anteroexternally, where in the earliest wear stages it is open through a shallow notch in the protoloph. The other two are small, shallow, nearly circular, about equal, and adjacent, one near the middle of the external moiety, the other just posterior to it. There are no distinct external, anterior, or internal cingula, but there is a strong basined posterior cingulum with a shallow posterointernal pit, becoming a coronal fossette with advanced wear, after the disappearance of the two minor external fossettes. P^4 is not molariform, and the transition to the molars is abrupt.

In dealing with the molar structure, a comparative review is most instructive. The majority of the *Pyrotherium* and *Colpodon* Beds



Fig. 8—Left upper molars of three early toxodont families in approximately equivalent wear stages. A, Notohippidæ (*Argyrohippus*). B, Rhynchippidæ (*Rhynchippus*). C, Nesodontidæ (*Nesodon*). Not to scale.

toxodonts (*sensu stricto*), with the exception of the Leontiniidæ, may be placed in three families, Rhynchippidæ, Notohippidæ, and Nesodontidæ. Each of these proves to have a characteristic molar pattern usually readily recognizable from unworn or moderately worn teeth. All are hypsodont, in degree depending rather on the age than on phyletic differences, but with closed roots. The Notohippidæ, but not the other two families, early developed a heavy cement coating on the cheek teeth.

In the Nesodontidæ, exemplified by *Proadinothierium* of the *Pyrotherium* and *Colpodon* Beds and by *Nesodon* of the Santa Cruz Formation, the molar pattern may be described as formed by a strong continuous ectoloph with five crests of different size and relation extending inward from it. The most anterior and distinct, clearly a true protoloph, extends to the internal border, where it ends freely until the very last stages of wear. The next, which may for descriptive purposes be called the first crista, reaches only to about the middle of the tooth, where it also ends

freely almost throughout its depth. The large anterior valley is thus open on the internal side almost throughout all wear stages, and is bifid at the outer end, its two branches resembling the prefossette and medifossette of the rhinoceros molar, for example, although not actually becoming closed fossettes even with advanced wear. The next two crests become united high on the crown at about the middle of the tooth, and the continuation inward from this point may be simple or may be unequally bifid at the internal side. A pit or fossette, closed even in early wear stages, is thus formed between these crests on the outer part of the tooth. For descriptive purposes, in spite of some question as to actual homology, the more anterior of these crests, where they are double, may be called the second crista, and the more posterior and the common inner part the metaloph. The fifth, and most posterior crest appears to arise phylogenetically as a cingulum. It extends from the ectoloph to the inner border, where it is united at a high point with the metaloph (except, usually on M^3), enclosing another posterointernal or median posterior fossette, which seems to correspond rather closely with the perissodactyl postfossette.¹

In the middle wear stages in the Nesodontidæ there are thus typically an anterior valley, open on the inner side and bifid externally, and two closed fossettes posterior to this.

The pattern in the Notohippidæ is typically closely similar to this, except that the first crista is united with the second crista nearly but not quite to its apex, at its inner end. In middle wear stages in this family, there are thus an anterior valley, similar to that in nesodonts but not bifid, and three closed fossettes external and posterior to this. The difference in itself is not very important, and the two conditions appear to intergrade to some extent, but it is fairly constant and characteristic of the two families.

In the Rhynchippidæ, as could not be seen on specimens known previously, the structure is more radically distinct from that of the Nesodontidæ. Protoloph and (nominal) metaloph and postfossette are much as in the two preceding families, but there is only one crista. This extends nearly to the inner border on apex of the unworn tooth, but retreats to near the middle of the crown as it continues toward the roots, as if crowded externally by the drawing together, and eventual fusion, in this direction of the inner ends of the protoloph and metaloph. Near the middle of the crown (considered transversely) and nearly to the apex,

¹As they arose quite independently, the word "homologous" seems to me inapplicable even where the same topographic nomenclature is conveniently used in such cases.

this crista is united to the metaloph, so as to enclose a single median external fossette. When moderately worn, the rhynchippid molar thus has an oblique main anterior valley, open at the inner border and not bifid at its anteroexternal end, and two small relatively shallow, closed fossettes, one median external and the other median posterior or postero-internal. With advanced wear the small fossettes disappear, the valley becomes closed on the inner side and is thus itself converted into a closed, long, narrow, curving pit or fossette. This is the condition figured by Loomis in *R. equinus*, while in Ameghino's figure of *R. pumilus* the condition is nearly the same except that the internal opening of the valley has not quite closed on the grinding surface of M^{2-3} . In this stage it gives little hint of the more complex apical pattern.

There are several ways in which the nothippid and nesodont pattern could be derived from the rhynchippid, but the reality of any one cannot be demonstrated without fuller phylogenetic data than that yet presented. That the three groups are rather intimately related and that the rhynchippids are on the whole the most primitive, are tenable working hypotheses.

Nothippidæ

Argyrohippus fraterculus Ameghino, 1902

The type of this genus does not appear to have been designated, the two species *A. boulei* and *A. fraterculus* being included in the original publication. There are obvious lapses or misprints in the measurements given, and the distinctions are not clear, so that the status of the species



Fig. 9—*Argyrohippus fraterculus* Ameghino. Amer. Mus. No. 29685. Crown view of left upper teeth. Three-fourths natural size.

and the identification of other specimens is still uncertain. To assist stabilization, I now designate *A. fraterculus* as genotype. Although placed after *A. boulei* in the original description, it was clearly considered by Ameghino to be the more characteristic, as it was this species, and not *A. boulei*, to which he several times referred in later publications and which he later figured.

Amer. Mus. No. 29685, found by C. S. Williams in the *Colpodon* Beds south of Lago Culhué-Huapi, clearly belongs in this genus and probably in this species. It is a skull, lacking the posterior part of the cranium but with the teeth well preserved. The dentition will not be described in detail at this time, but is figured. The essential molar characters, as mentioned above, are the heavy cement and the presence of two cristæ united nearly to their apices. The family appears to represent a valid phylum, of rather close common origin with the nesodontids.

REFERENCES

- AMEGHINO, F. 1897. Mammifères crétacés de l'Argentine. (Deuxième contribution à la connaissance de la faune mammalogique des couches à *Pyrotherium*). Bol. Inst. Geog. Arg., XVIII, pp. 406-429, 431-521. [Also as a separate, pp. 1-117.]
1902. Première contribution à la connaissance de la faune mammalogique des couches à *Colpodon*. Bol. Ac. Nac. Ci. Córdoba, XVII, pp. 71-138.
- LOOMIS, F. B. 1914. The Deseado Formation of Patagonia. Amherst, Mass.
- SCOTT, W. B. 1910. Litopterna of the Santa Cruz Beds. Rept. Princeton Exp. Patagonia, VII, Pt. I, pp. 1-156.

